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REPORT

Near-surface enrichment of zooplankton over a shallow back reef: implications for coral reef food webs

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Abstract Zooplankton were 3–8 times more abundant during the day near the surface than elsewhere in the water column over a 1–2.4 m deep back reef in Moorea, French Polynesia. Zooplankton were also significantly more abundant near the surface at night although gradients were most pronounced under moonlight. Zooplankton in a unidirectional current became concentrated near the surface within 2 m of departing a well-mixed trough immediately behind the reef crest, indicating that upward swimming behavior, rather than near-bottom depletion by reef planktivores, was the proximal cause of these gradients. Zooplankton were highly enriched near the surface before and after a full lunar eclipse but distributed evenly throughout the water column during the eclipse itself supporting light as a proximal cue for the upward swimming behavior of many taxa. This is the first investigation of the vertical distribution of zooplankton over a shallow back reef typical of island barrier reef systems common around the world. Previous studies on deeper fringing reefs found zooplankton depletion near the bottom but no enrichment aloft. In Moorea, where seawater is continuously recirculated out the lagoon and back across the reef crest onto the back reef, selection for upward swimming behavior may be especially strong, because the surface serves both as a refuge from predation and an optimum location for retention within the reef system. Planktivorous fish and corals that can forage or grow even marginally higher in the water column might have a substantial competitive advantage over those nearer the bottom on shallow reefs. Zooplankton abundance varied more over a few tens of centimeters vertical distance than it did between seasons or even between day and night indicating that great care must be taken to accurately assess the availability of zooplankton as food on shallow reefs.

Keywords Coral reef zooplankton · Zooplankton distribution · Lunar eclipse · Moorea · French Polynesia · Coral feeding · Planktivorous fish · Vertical migration

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Introduction

Zooplankton are a central link in the food webs of coral reefs and are the focus of intense predation by reef consumers (Erez 1990). They serve as food for many fishes (Hobson and Chess 1978; Hamner et al. 1988), corals (Sebens et al. 1998; Palardy et al. 2006), and sessile invertebrates (Sebens and DeRiemer 1977; Kappner et al. 2000). Since many zooplankton consumers are either attached to the bottom or, if motile, forage near shelters on the bottom, the vertical distribution of zooplankton in the water column is a critical factor in determining consumer feeding rates, foraging behavior, and prey availability.

Recent studies have reported near-bottom depletion of pelagic zooplankton over reefs. Zooplankton exhibited substantial depletion in the layer within 1.5 m of the bottom on 8–14 m deep reefs in the Red Sea both day and night with relatively homogeneous distributions higher in the water column (Yahel et al. 2005; Holzman et al. 2005). Both higher consumption of zooplankton near the reef and avoidance of the bottom by more strongly swimming

zooplankton contributed to the strong vertical gradients in zooplankton distribution observed in these studies (Holzman et al. 2005; Motro et al. 2005). Higher predation intensity near the reef appears to be the ultimate selective pressure generating near-bottom depletion of zooplankton (Holzman et al. 2005; Motro et al. 2005).

These recent studies were conducted on deep fringing reefs. Little is currently known regarding the vertical distribution of zooplankton in the water columns of the very shallow back reefs typical of island barrier reef systems around the world. These systems are characterized by greater water retention and entrainment (Hench et al. 2008). They harbor diverse guilds of hyperbenthic (Emery 1968; Carleton and Hamner 2007), demersal (Alldredge and King 1977), and endemic zooplankton as well as offshore holoplankton that have, over many generations, become resident (Roman et al. 1990; Leichter et al. 1998). Resident holoplankton and demersal forms would be expected to have evolved behavioral mechanisms to avoid the intense predation near the bottom. Information on the vertical distributions of zooplankton over shallow back reefs is essential for understanding the food availability, foraging behavior, and food web dynamics of corals, fishes and other planktivores. It may also provide insight into the mechanisms by which zooplankton gradients are generated and maintained.

The vertical distribution of zooplankton on the shallow back reef of the north shore of Moorea, French Polynesia was investigated in association with the Moorea Coral Reef Long Term Ecological Research (LTER) program. Three major questions were addressed: (1) Do zooplankton show vertical gradients over shallow reefs only 1–3 m deep? (2) Are these gradients generated by zooplankton swimming behavior or by depletion from more intense consumption of zooplankton near the bottom? (3) What environmental cues (e.g., proximal causes) might generate any gradients in zooplankton abundance observed?

Materials and methods

Study site

Zooplankton collections were made primarily at two stations on the shallow back reef of the north shore of Moorea, French Polynesia. In this system, a very shallow reef crest (20 cm deep and ~3–6 m wide) separates the fore reef from a shallow (1–3 m deep) back reef extending almost 1 km behind the crest to the shore of the island. Sampling occurred primarily along a 32 m transect starting at the trough directly behind the reef crest at 17°28.644″S, 149°50.536″W and extending perpendicular to the crest over the back reef, and at a single site 110 m behind the reef crest at 17°28.706″S, 149°50.534″W (Fig. 1). These

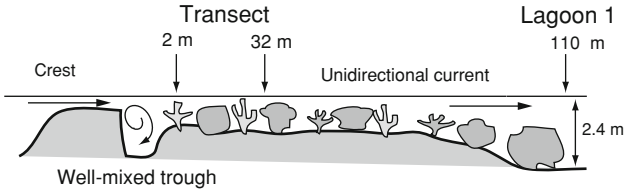

Fig. 1 Cross-sectional view of the two major study sites and their distances from the trough on the back reef of the north shore of Moorea, French Polynesia

two sites will be referred to as "Transect" and "Lagoon 1." Lagoon 1 is regularly investigated by the Moorea Coral Reef LTER. A unidirectional current largely driven by wave forcing and varying from 5 to >30 cm s^{-1}, depending on season, flows across the back reef toward the island shore all year (Hench et al. 2008). Tides are very small in amplitude (0–0.2 m) and, because of significant solar influence, nearly constant, with a high tide close to noon and midnight each day (Hench et al. 2008).

The trough directly behind the reef crest was 1.5–2 m wide and 1.5–2 m deep and contained rubble and broken coral fragments. Living corals, especially *Porites lobata* and *Acropora, Montastrea, Pocillopora*, and *Millepora* spp., pavement, rubble, and crustose coralline algae occurred along the 1.1–1.2 m deep "Transect" behind the crest, with only 10% coral cover in the 2–3 m directly behind the trough at the sampling locations. Lagoon 1 was 2.2–2.4 m deep with 25 ± 22% cover by *Porites lobata* (LTER Public Data, http://mcr.lternet.edu/data). Coral rubble, sand patches, scoured reef pavement with crustose coralline algae, turf, and scattered corals of the genera *Pavona, Montipora*, and *Pocillopora* also occurred there. A third station 8 m deep on the fore reef across from Lagoon 1 was also sampled for comparison (17°28.5″S, 149°50.226″W). This station had 43 ± 13% coral cover by a diverse assemblage of living corals especially *Acropora, Montastrea*, and *Pocillopora* species and rarer *Leptastrea, Fungia*, and *Pavona* spp. separated by pavement (LTER Public Data, http://mcr.lternet.edu/data). Common diurnal planktivorous fishes seen at our sites included numerous pomacentrid species (*Abudefduf sexfasciatus, Chromis* spp., *Dascyllus* spp.), triggerfish (*Melichthys* spp., *Odonus niger*), and wrasses (*Pseudocheilinus* sp., *Thalassoma* spp.). Nocturnal planktivores included soldier fishes (*Myripristis* spp.) and cardinal fishes (*Apogon* spp., *Cheilodipterus* spp.).

Sampling methods

Three types of samples were used in this study: plankton pumps, nets, and moored nets. All zooplankton samples were preserved in 2% buffered formalin and later counted and identified to major taxa with a dissecting microscope.

Where necessary, samples were split with a Folsom plankton splitter.

Plankton pumps

Plankton pumps were modified from the design of Sebens et al. (1992). Each pump consisted of a 10 cm diameter, 46 cm long PVC tube containing a 30 cm long plankton net of 200 µm mesh and a cod end consisting of a 250 ml screw-on, polypropylene bottle with mesh openings (Fig. 2). A small funnel sat inside the cod end to help prevent zooplankton from swimming out once captured. Seawater, pumped by a Rule 2000 bilge pump behind the cod end, entered the net through a 2.54 cm diameter intake pipe of variable height above the bottom and exited the pump through a Dwyer Model TTM11 Totalizer, which digitally recorded the volume sampled. The bilge pump was powered by a 12 v, 17 amp gel battery in a water tight box and controlled by a DIG Irrigation Products Hose Thread Watering Timer model 9001DB, which could be programmed to sample at any time and duration desired. Seawater volumes of 4–5 m^3 were sampled over 1–1.3 h pump duration in this study. Digital movies of carmine dye placed near the intake revealed that these pumps sampled ±7 cm above and below the intake. No sampling bias has been reported for similar pumps collecting zooplankton <1 mm in size (Yahel et al. 2005; Sebens et al. 1998). Pumps sampling at five heights at Lagoon 1 on two different days yielded mean water column abundances similar to diver-swum nets sampling simultaneously (mean abundances of 62.5 and 56.8 animals m^{-3} on day one and 21.3 and 24.6 animals m^{-3} on day 2 for pumps and nets, respectively) in support of this assertion.

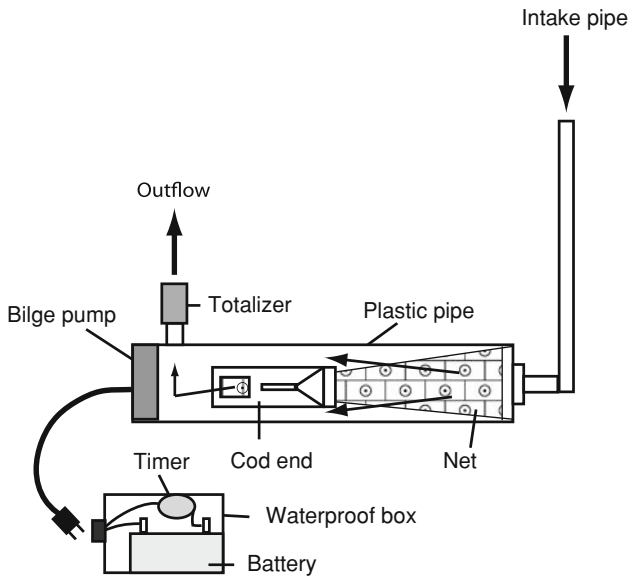

Fig. 2 Automated plankton pump used to sample zooplankton. The length of the intake pipe was varied to sample at different heights above the bottom

Diver-swum 2-net array

Two, 200 µm mesh, plankton nets 30 cm long with rectangular mouth openings of 20 × 14.6 cm (0.0292 m^2) were clamped 50 cm apart (center to center) on a plastic pipe. The top net contained a General Oceanic's Model 2030 flow meter. This two-net array was swum by a snorkeler with the top of the upper most net placed 5–10 cm below the surface, allowing simultaneous collection of zooplankton at two depths, near surface, and 70 cm deep. Nets were swum for 15–20 min to sample 7–10 m^3.

Moored net array

A consistent unidirectional current of 5–35 cm s^{-1} at the study site (Fig. 1; Hench et al. 2008) allowed use of moored nets to assess zooplankton distributions over more integrated time periods. Two, 30 cm diameter, 300 µm mesh nets were tied one on top of the other to a subsurface float moored to the bottom. (A larger mesh size was used to avoid excessive clogging). The cod ends contained inverted funnels to deter escape of animals. The nets were moored on a swivel and held horizontally by rods linking the cod ends and mouth rings, allowing them to fish like wind socks in the current.

Studies

Vertical Plankton distributions

The distribution of zooplankton in the water column was determined at Lagoon 1 using pumps sampling at 15, 50, 100, 150, and 200 cm above the bottom, during midday (1100–1200 hours) and midnight (2300–2400 hours) on the new, first, full, and third quarter moons during August and September of 2007 and 2008, new moon in January 2008 and full and third quarter moons during January 2009. The diver-swum 2-net array was also used to sample the fore reef during the day in August 2008 at depths of 50, 100, 150, 200, and 800 cm (near surface) above the bottom. A weighted line tied to the bottom net was kept in contact with the bottom while sampling to insure collection at the desired height.

Test of consumption by the reef versus zooplankton swimming behavior

If consumption by reef-associated planktivores (corals, fish, and sessile invertebrates) was a significant cause of any gradients observed, then zooplankton would become

gradually more depleted near the bottom with distance from the well-mixed trough, because the further zooplankton were swept from the trough by the unidirectional current, the longer their exposure to predation near the bottom. During this study, the transect experienced relatively slow flow with little mixing beyond the trough. Alternatively, if zooplankton concentrated at the surface soon after exiting the trough, then swimming behavior would better explain any vertical gradients observed.

Divers simultaneously sampled near the surface and 70 cm below the surface with the 2-net array along transects parallel to the reef crest in the trough and at distances of 2, 12, and 32 m behind the trough at 0930–1030 hours on August 26, 2007, and in the trough and at 3, 8, 14, and 20 m behind the trough at 0930–1030 hours on September 2, 2007. We also placed two moored net arrays at 3 m and 11 m behind the trough from 1040 to 1400 hours and at 8 and 15 m behind the trough from 1405 to 1700 hours on August 31, 2007. Net openings were centered at 25 and 70 cm below the surface (bottom depth 100–120 cm). Nortek Aquadopp current profilers, placed on the bottom near the nets at 3 and 11 m from the trough measured average current velocities at binned depths throughout the water column every 6 min in order to estimate flow through the nets. Since the top and bottom nets experienced slightly different flow because current velocities decreased slightly nearer the bottom, zooplankton collections from moored nets were normalized to the mean current flow in order to compare them accurately.

Effects of light

The importance of light as a cue was tested in two studies:

Plankton distributions at quarter moon If light was an important cue determining vertical distributions, then zooplankton should have different distributions when the moon was up then when the moon was down on the same night. Lagoon 1 was sampled with pumps on the nights of August 21, 2008, and January 16, 2009, during the third quarter moon at heights of 40, 125, and 200 cm above the bottom from 2030 to 2130 hours while the moon was down and from 0230 to 0330 hours while the moon was up. The moon rose at 2237 hours and 2255 hours local time on August 21 and January 16, respectively, and was high in the sky during the moonlit sampling period.

Lunar eclipse Moorea experienced a total lunar eclipse during the full moon on August 27, 2007. The eclipse entered umbra at 2152 hours, entered totality at 2352 hours, left totality at 0122 hours, and ended (left umbra) at 0223 hours. Sampling occurred using plankton pumps at only two heights, 55 and 155 cm, above the bottom (due to limitation on the number of pumps available) at Lagoon 1 before (2030–2130 hours), during totality (2400–0100 hours), and after (0330–0430 hours) the eclipse and at the same times and heights on the control night of August 28, 2007.

Phytoplankton distributions

Sixty milliliters of seawater samples were collected at 15, 50, 100, 150, and 200 cm above the bottom by snorkelers while plankton pumps were sampling during daylight on January 10 and August 15, 2008, to assess the distribution of phytoplankton, a potential food source for many zooplankton and microzooplankton. Samples were preserved in 0.2% hexamine-buffered formalin, settled in 50 ml settling columns, and counted using the Utermohl method on an inverted microscope.

Statistics

The statistical significance of vertical gradients in zooplankton abundance and biomass were determined using the Page Test for Ordered Alternatives (Siegel and Castellan 1998). This nonparametric test is a modified version of the Kruskal–Wallis one-way ANOVA of ranked data. Means of day and night samples were compared using one-way analysis of variance with the Holm–Sidak post hoc method for pairwise multiple comparisons. Means were log transformed to meet the requirement for homogeneity of variances.

Results

Copepods were the most abundant taxon during the day, averaging 72–83% of total zooplankton numbers. These included diverse harpacticoid taxa, small paracalanids, cyclopoids, and the predatory copepods such as *Labidocera*. Gastropod veliger larvae, larvaceans, polychaetes, and occasional crustacean larvae also occurred (Table 1). Large crustacean larvae, dominated by crab zoea, crab megalopae, and decapod larvae were much more abundant at night than during the day. Copepods made up from 26 to 49% of the nocturnal zooplankton, averaging 36%, while crustacean larvae made up 31–71%, averaging 41%. Veliger larvae were the next most abundant group ranging from 3 to 18% of the total nocturnal plankton, averaging 12%. Isopods, parasitic gnathiid isopods, amphipods, tanaids, polychaetes, ostracods, fish larvae and occasional small shrimp, and the cephalochordate, *Branchiostoma* sp., were also common at night (Table 1).

Total daytime zooplankton abundance was low and not significantly different from nighttime abundance when the

Table 1 Mean abundance ± standard deviation, mean organic carbon content ± standard error (number animals assayed) and length of the major zooplankton taxa in the water column at Lagoon 1

Taxon	Day (No. m^{-3})	Night moon down (No. m^{-3})	Night moon up (No. m^{-3})	Mean POC content (ug C $animal^{-1}$)	Size range (mm)
Copepods	41.7 ± 45.2	23.0 ± 15.4	31.7 ± 38.3	4.6 ± 0.3 (92)	0.4–1.2
Labidocera	0.2 ± 0.6	0.6 ± 1.5	0.5 ± 0.6	42.4 ± 5.6 (33)	1.5–2.5
Crab zoea	2.1 ± 5.9	4.2 ± 4.9	61.4 ± 94.2	4.0 ± 0.3 (63)	0.7–1.2
Crab megalopae	0	2.2 ± 2.4	0.8 ± 1.2	69.8 (7)	0.8–4.2
Decapod larvae	0.5 ± 0.7	9.2 ± 10.6	6.6 ± 9.7	17.9 ± 9.0 (103)	1.1–3.0
Amphipods	0.3 ± 0.6	1.1 ± 1.4	1.4 ± 1.9	26.6 ± 4.5 (28)	1.0–3.0
Isopods	0.3 ± 0.7	0.8 ± 0.8	0.9 ± 0.9	8.3 (11)	0.9–2.5
Gnathiid isopods	0	0.3 ± 0.5	0.6 ± 1.0	32.0 ± 7.1 (15)	1.3–2.6
Mysids	0.1 ± 0.2	1.9 ± 2.2	0.6 ± 1.0	28.8 ± 4.6 (29)	1.4–2.5
Ostracods	1.0 ± 1.6	1.9 ± 5.2	1.3 ± 2.3	15.6 ± 3.4 (69)	0.2–1.2
Tanaidaceans	0.1 ± 0.2	0.1 ± 0.3	0.1 ± 0.4	5.0 (12)	0.9–1.8
Shrimp	0	1.0 ± 0.9	0.3 ± 0.4	120.2 ± 33.1 (26)	3.2–7.0
Veliger larvae	7.7 ± 9.6	5.5 ± 7.2	5.9 ± 6.1	2.4 ± 0.3 (63)	0.2–0.5
Polychaetes	1.5 ± 6.0	3.9 ± 6.3	4.2 ± 8.4	43.8 (6)	0.7–6.0
Fish larvae	0	0.2 ± 0.5	0.2 ± 0.4	339.0 ± 128 (8)	2.5–7.0
Amphioxus sp.	0	0.9 ± 2.1	0.2 ± 0.4	68.3 ± 22.5 (10)	5.0–5.2
Larvaceans	2.1 ± 9.8	0.4 ± 1.7	0.9 ± 2.3	3.5 ± 0.2 (50)	0.4–1.5
Chaetognaths	0.1 ± 0.4	0.1 ± 0.2	0.2 ± 0.6	133.4 ± 45.9 (13)	3.2–5.9
Miscellaneous	1.4 ± 1.5	1.8 ± 2.0	1.9 ± 2.0		
Total	59.3 ± 16.8	57.8 ± 10	119.4 ± 58.0		

Standard deviations of abundances are high because of the large differences in abundance with height above the bottom

moon was down, ranging from 20 to 189 animals m^{-3} (depending on depth) and averaging 59 ± 17 animals m^{-3} ($n = 8$) and 58 ± 10 animals m^{-3} ($n = 8$) throughout the water column during days and moonless nights, respectively (Table 1). However, when the moon was up, and especially at full moon, average total abundance was significantly higher ($P < 0.01$, $n = 6$) by 2 to 4 times, ranging from 28 to 366 animals m^{-3} and averaging 119 ± 59 animals m^{-3}. In contrast, the total biomass of plankton was 2–4 times higher at night than during the day ($P < 0.001$), but not significantly different with moon state averaging 0.3 ± 0.08 mg POC m^{-3}, 1.1 ± 0.5 mg POC m^{-3}, and 1.0 ± 0.3 mg POC m^{-3} during daylight, moonless, and moonlit nights, respectively. Biomass during moonless and moonlit periods was similar despite differences in abundance between these periods due to the predominance of larger zooplankton, primarily megalopae, decapod larvae, and amphioxus when the moon was down (Table 1).

Vertical plankton gradients

During daylight total zooplankton, predominantly small copepods and veliger larvae, were 3–8 times higher in abundance and total biomass near the surface than at midwater or near-bottom depths in water only 2.4 m deep. This pattern was highly significant ($P < 0.001$) and seen on all sampling days. Abundances were several times higher in the upper 50 cm of the water column, especially during calm days (Fig. 3a). Under wind-induced wave chop of 10–20 cm and mixing, zooplankton enrichment extended throughout the upper 1 m of the water column (Fig. 3b). Enrichment near the surface was a general pattern seen in all diurnal taxa except isopods and amphipods (Table 2). No zooplankton were ever observed swarming near the bottom.

Total zooplankton abundance was also significantly higher nearer the surface at night ($P < 0.001$, $n = 14$ nights, Table 2) although gradients were not as pronounced as during the day, especially at new moon. But biomass was up to eight times higher near the surface than elsewhere in the water column at night because larger taxa aggregated near the surface (Fig. 4). This overall pattern was not affected by moonlight. Significantly, more total zooplankton and biomass occurred nearer the surface both when the moon was up and when the moon was down ($P < 0.001$). Crab zoea, crab megalopae, ostracods, veliger larvae, polychaetes, and larvaceans were all significantly higher in abundance near the surface regardless of the presence of moonlight (Table 2). Nevertheless, moonlight did strongly affect the distribution of two of the most

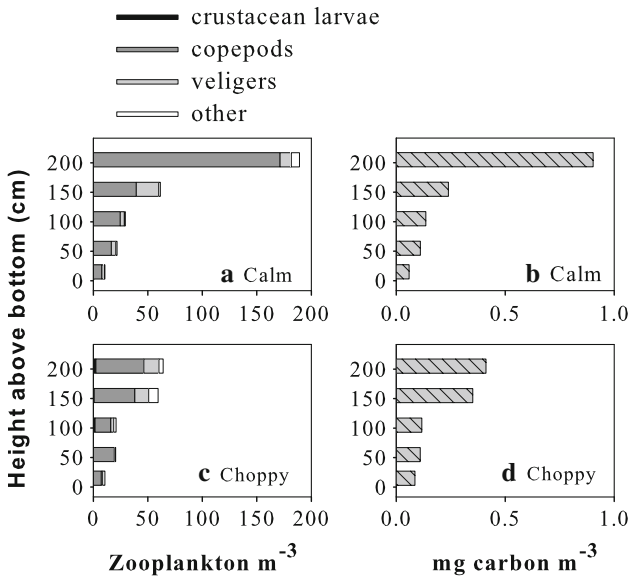

Fig. 3 Examples of typical day time vertical distributions of zooplankton abundance and total biomass (as organic carbon) in the 2.4 m deep water column at Lagoon 1 under calm and choppy wave conditions. **a**, **b** August 16, 2007; **c**, **d** September 6, 2007

Table 2 Statistical results of the page test for ordered alternatives for enrichment toward the surface of various taxa during the day and at night

Taxon	Day ($n = 8$)	Moon up ($n = 6$)	Moon down ($n = 8$)
Copepods	Yes**	Yes***	No
Decapod larvae	–	Yes*	No
Zoea	Yes**	Yes***	Yes***
Megalopae	–	Yes*	Yes**
Amphipods	No	No	No
Isopods	No	No	No
Gnathiid isopods[a]	–	Yes**	Yes**
Mysids	–	No	No
Ostracods	Yes**	Yes*	Yes**
Veliger larvae	Yes**	Yes*	Yes**
Polychaetes	Yes*	Yes*	Yes***
Larvaceans	Yes**	Yes***	Yes***
Total Plankton	Yes***	Yes***	Yes***

Some taxa are not listed because they occurred too rarely to assess. Yes, significantly stratified; no, not significantly stratified

* Significant at $P < 0.05$, ** significant at $P < 0.01$, *** significant at $P < 0.001$

[a] Abundance gradient reversed (significantly higher toward bottom)

abundant taxa, copepods and decapod larvae. These taxa were not significantly stratified when the moon was down in part because of slightly elevated concentrations right above the bottom (Table 2), but were significantly

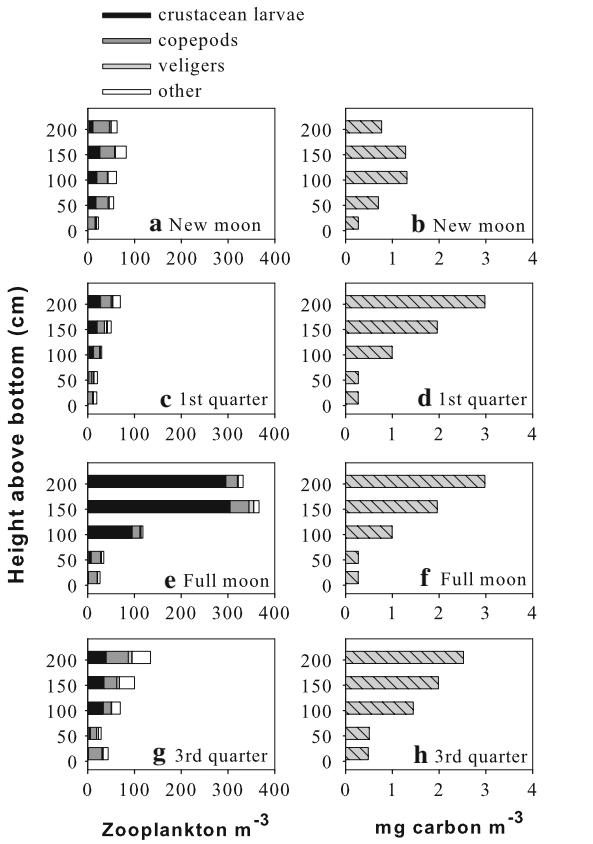

Fig. 4 Examples of typical night time vertical distributions of zooplankton abundance and total biomass (as organic carbon) in the 2.4 m deep water column at Lagoon 1 over the lunar cycle in August and September 2007

aggregated near the surface when the moon was up (Table 2, Fig. 4e, g).

Four taxa did not follow this general pattern. As during the day, isopods, amphipods, and additionally mysids were not significantly higher in abundance at any depth (Table 2). Gnathiid isopods, the juveniles of which are parasitic on fish, showed a reverse pattern, occurring only in the lower 1 m of the water column, with significantly higher abundance within 50 cm of the bottom ($P < 0.01$, Fig. 5).

Causes of observed zooplankton gradients

Zooplankton became stratified in abundance very rapidly along the transect immediately behind the reef crest. Water depth along this transect varied from 1.0 to 1.2 m (Fig. 2). Zooplankton were similar in abundance at 15 cm below the surface and 70 cm below the surface in the well-mixed, 1.5 m deep trough directly behind the reef crest. However, by 2–3 m beyond the trough, zooplankton were already twice as abundant near the surface as near the bottom (Fig. 6) suggesting that the zooplankton swam upward. At

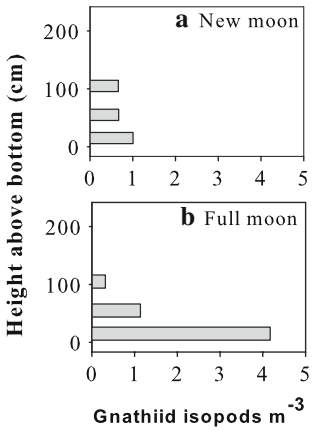

Fig. 5 Examples of typical night time vertical distributions of gnathiid isopods in the 2.4 m deep water column at Lagoon 1 during the new and full moons of August 2007

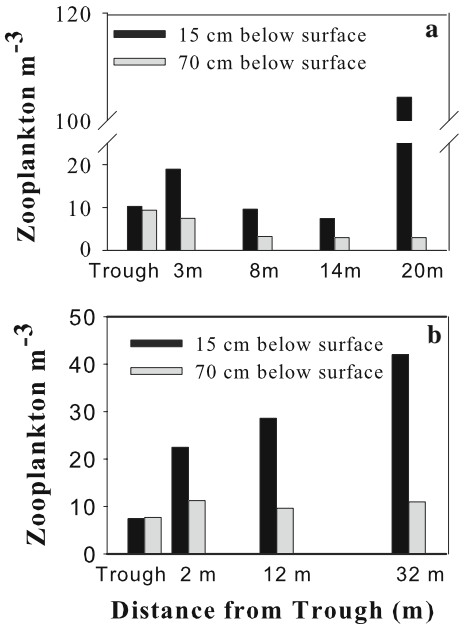

Fig. 6 Daytime abundance of total zooplankton at 15 cm and 70 cm below the surface along a 1.1–1.2 m deep transect extending from the trough behind the reef crest toward shore. **a** September 7, 2007, **b** August 26, 2006

measured current velocities averaging 8.6 cm s^{-1}, zooplankton required only 23 s to be carried 2 m beyond the trough and 34 s to be carried 3 m beyond the trough.

Drift net collections yielded an identical result. The horizontal flux of zooplankton was higher near the surface just 2 m beyond the well-mixed trough and by 11 m beyond the trough (2.2 min by current flow), 80% of the zooplankton flux was found in the near-surface net (Fig. 7a). Zooplankton flux was normalized to the mean current velocity of 8.6 ± 3.0 cm s^{-1} to compensate for the slightly higher current flow near the surface.

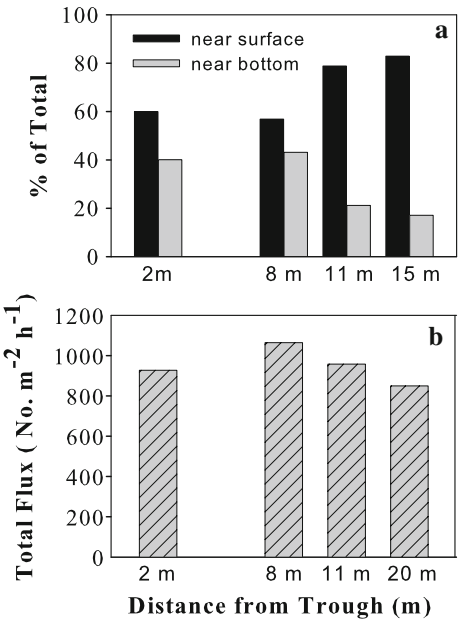

Fig. 7 Horizontal daytime flux of zooplankton carried by a unidirectional current into moored nets centered at 25 and 70 cm below the surface along a 1.1–1.2 m deep transect that extended from the edge of the trough behind the reef crest toward shore on August 31, 2007. **a** Percentage contribution of each net to total zooplankton flux. **b** Mean total zooplankton flux at various distances from the trough

Diver-swum nets suggested considerable heterogeneity in zooplankton abundance along the transect (see Fig. 6). However, the drift nets, which sampled more of the water column over several hours, averaged this heterogeneity and revealed that mean zooplankton flux was similar regardless of distance from the trough with no evidence of zooplankton depletion by the reef over the short horizontal distance investigated (Fig. 7b).

Effects of light

The more homogeneous vertical distribution of copepods and decapod larvae during moonless periods and the strong gradients in abundance occurring under full moon and daylight suggested that upward swimming behavior in response to light might be a proximal cause for accumulation of zooplankton nearer the surface. We tested this hypothesis in two ways.

Third quarter moon

We compared the vertical distribution of zooplankton before and after moonrise during third quarter moon. Both replicate nights (August 2008 and January 2009) yielded similar results, and we report those for August 21, 2008, in Figs. 8 and 9. Total zooplankton were more abundant near the surface both before and after moonrise (Fig. 8).

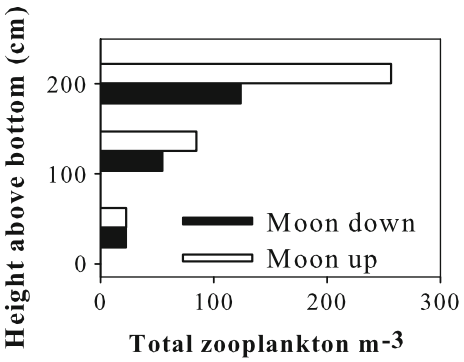

Fig. 8 Vertical distribution of total zooplankton abundance during moonlit and moonless periods of the third quarter moon on August 21, 2008, in the 2.4 m deep water column at Lagoon 1

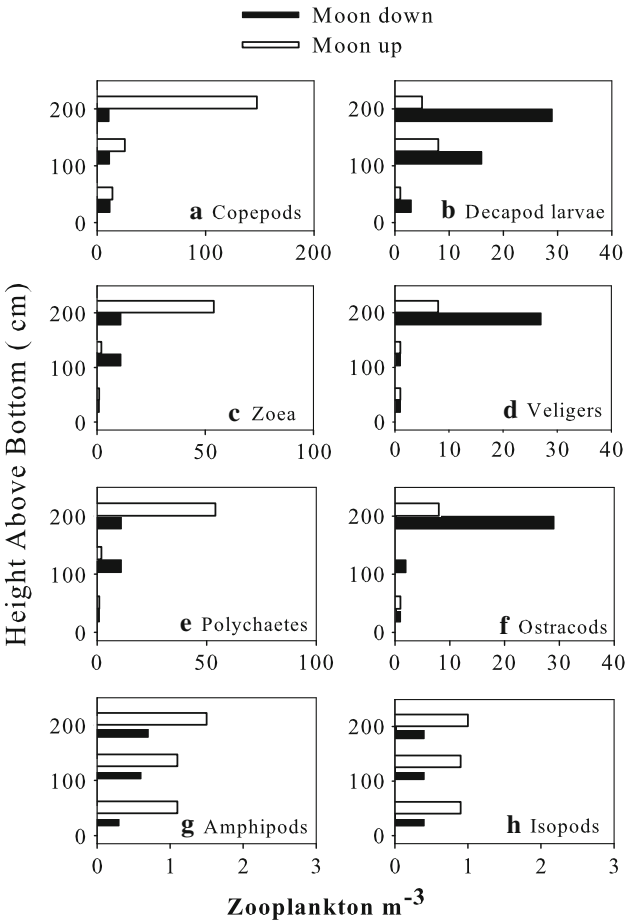

Fig. 9 Vertical distribution of various zooplankton taxa during moonlit and moonless periods of the third quarter moon on August 21, 2008, in the 2.4 m deep water column at Lagoon 1. A repeat of this study on January 20, 2009, yielded similar results

However, four basic behavior patterns generated this overall trend:

1. *Taxa with a strong positive response to light*—Copepods (Fig. 9a), crab zoea (Fig. 9c), and polychaetes (Fig. 9g) were much more abundant when the moon was up and 80–95% of individuals in these taxa occurred near the surface. When the moon was down, they were more uniformly distributed throughout the water column, especially in the upper half.
2. *Taxa that swam up in the dark and avoided moonlight*—Decapod larvae (Fig. 9b), veliger larvae (Fig. 9d), and ostracods (Fig. 9f) were enriched near the surface regardless of the moon. However, they were much higher in total abundance when the moon was down.
3. *Taxa with no response to light*—Amphipods (Fig. 9g) and non-gnathiid isopods (Fig. 9h) were relatively uniformly distributed throughout the water column regardless of the moon state. As in the daytime, these taxa did not appear to respond to light.
4. *Taxa that stayed near the bottom*—The behavior of gnathiid isopods during the third quarter moon was similar to that seen during other moon states (see Fig. 5). They remained closer to the bottom when the moon was up just as they did during full moon (Fig. 5).

Moonlight strongly affected plankton community composition. Copepods and zoea, among the smallest taxa, dominated the plankton when the moon was up while larger taxa including ostracods, veligers, and decapod larvae were predominant when the moon was down (Fig. 9).

Response to the lunar eclipse

Zooplankton were 2–4 times more abundant near the surface throughout the full moon control night (Fig. 10a). However, while zooplankton were 2–4 times more abundant near the surface before and after the eclipse (66–80% near the surface), without the light cue from the full moon during the eclipse (2152–0223 hours) they redistributed more homogeneously, with only 41% nearer the surface and 59% nearer the bottom (Fig. 10b). All the taxa showed this same pattern of slightly higher abundance near the bottom during the totality of the lunar eclipse including decapod larvae, veliger larvae, ostracods, amphipods, and isopods, suggesting that even these taxa had some responsiveness to light. The only exception was gnathiid isopods, which remained near the bottom throughout both nights.

Phytoplankton food

Most phytoplankton, predominantly small (<5 um) naked flagellates too small for most zooplankton to consume, were evenly distributed vertically throughout the water column (Fig. 11). Rare larger phytoplankton, predominantly small benthic pennate diatoms similar to *Navicula* sp., were twice as abundant near the bottom, while zooplankton collected simultaneously were enriched near the surface (Fig. 11).

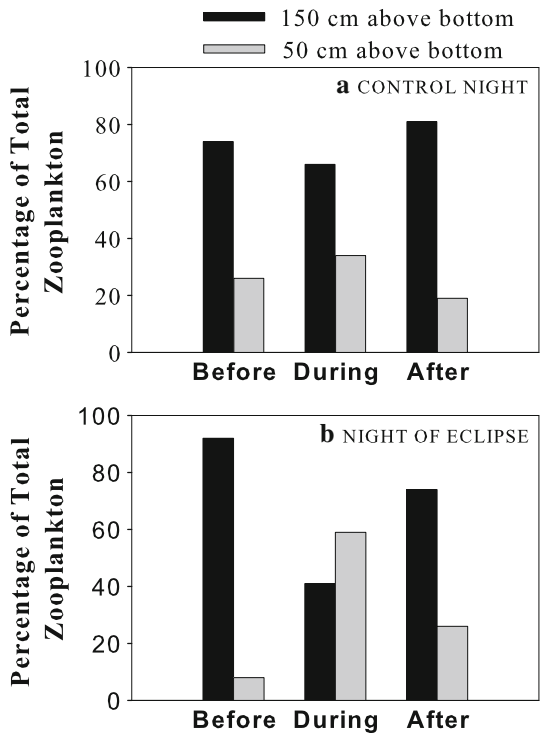

Fig. 10 The percentage of zooplankton in the 2.4 m water column found near the surface and near the bottom **a** before, during and after a full lunar eclipse of the full moon on August 27, 2007, and **b** on the control night of August 28, 2007

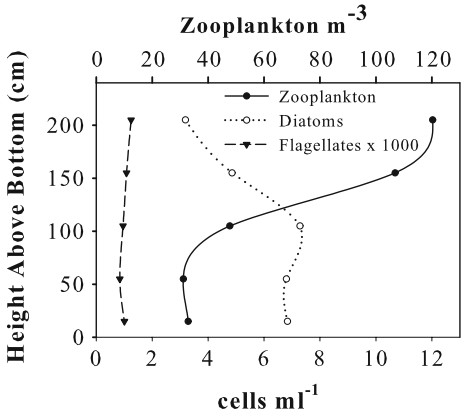

Fig. 11 Example of the typical vertical daytime distribution of phytoplankton and zooplankton in the 2.4 m deep water column at Lagoon 1. Data shown for August 15, 2008. Flagellates consisted of small (<5 um) naked cells

Fore reef distributions

While this study did not focus on the fore reef, we did sample there in order to better understand the delivery of plankton across the reef crest to the lagoon. Zooplankton were four times more abundant near the surface at 8 m above the reef during the day than at 2 m above the reef and about eight times higher than at 1 m above the reef

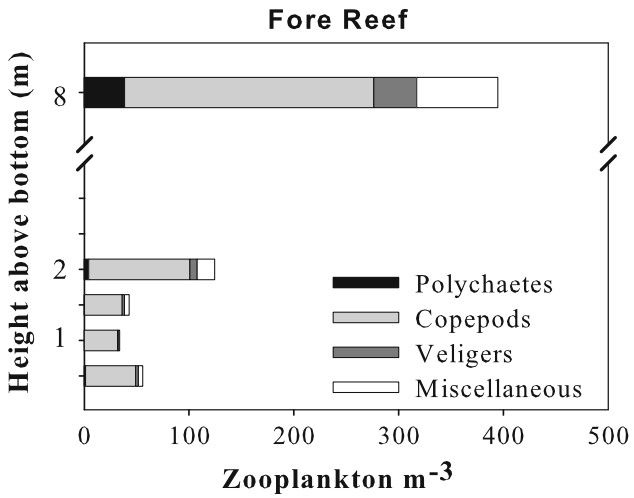

Fig. 12 Daytime vertical distribution of zooplankton abundance on the 8 m deep fore reef across the reef crest from the back reef study sites on August 30, 2008

(Fig. 12). Daytime plankton on the fore reef was dominated by copepods, veligers, polychaetes, and larvaceans.

Discussion

This is the first study to investigate the vertical distribution of zooplankton over a shallow back reef typical of many barrier reefs island systems around the world. It revealed that zooplankton were highly enriched near the surface, both day and night even in water only 1–2.4 m deep. This pattern was general rather than taxon specific suggesting that common selective pressures act to structure the zooplankton community. Previous published studies have reported near-bottom depletion but no surface enrichment above deep fringing reefs (5–15 m) of the Red Sea (Yahel et al. 2005); although one unpublished study did find some surface enrichment off Florida (Heidelberg, personal communication). The surface in shallow water may serve both as a refuge and a barrier to further upward swimming. Our results shed light on both the proximal and ultimate causes of these zooplankton gradients.

Proximal causes of zooplankton surface enrichment

Predation on coral reef zooplankton is higher near the bottom where corals and other sessile planktivores feed and planktivorous fish shelter from reef piscivores (Hobson 1991). Thus, consumption is one explanation for near-bottom depletion of zooplankton (Yahel et al. 2005; Holzman et al. 2005) and vertical gradients in fish predation pressure on zooplankton support this mechanism (Motro et al. 2005). However, upward swimming behavior appears to be the proximal cause of the near-surface

enrichment of zooplankton in Moorea. Zooplankton developed strong vertical gradients in abundance within 23 s of exiting the well-mixed trough in a unidirectional current. Only zooplankton swimming behavior can explain the rapid near-surface enrichment observed since consumers, including sparse corals (which were not feeding in daylight) and a few damselfish, were far too rare in the 2 m behind the trough to account for this large change.

This point can be further illustrated with what little data are available on zooplankton consumption rates by corals. Palardy et al. (2006) found maximum feeding rates of 0.2 zooplankton cm^{-2} (of coral surface) h^{-1} for the mounding coral *Pavona gigantea* at low zooplankton concentrations similar to those at our study site. At a mean current speed of 8.6 cm s^{-1} and 10% cover of mostly the mounding coral *Porites lobata*, the corals in the 2 m^2 area directly behind the trough at our transect site might consume two zooplankton in the 23 s required for the current to carry the plankton across this area. This is about 3% of the plankton moving past the corals in that time interval and far too low to explain the twofold higher abundance of zooplankton near the surface found just 2 m behind the trough. Consumption becomes even more improbable a cause when we consider that the corals were not feeding in the daytime when we sampled and most corals rarely consume copepods (Palardy et al. 2006; Sebens et al. 1996), which made up >75% of our samples. Other sessile suspension feeders, such as ascidians and sponges, were extremely rare.

Coral reef zooplankton are capable of swimming many body lengths per second and can swim effectively against upwelling and downwelling currents (Genin et al. 2005). Small pelagic copepods can cruise at 0.5–0.9 cm s^{-1} (Yen et al. 2008) with average escape speeds of >25 cm s^{-1} (Visser et al. 2009), indicating they would be fully capable of swimming to the surface of a 1–3 m water column within seconds to minutes. Likewise the swimming speeds of other common zooplankton including veliger larvae (0.1–1 cm s^{-1}), polychaetes (0.1–0.5 cm s^{-1}), and zoea (0.8–2 cm s^{-1}) (Mileikovsky 1973) are adequate to easily propel them quickly to the surface in shallow water. Consistent with our results, the strongest swimmers, especially copepods and polychaetes, also showed the strongest gradients in the depleted near-bottom zone in the Red Sea (Holzman et al. 2005).

Several environmental cues could invoke upward swimming of zooplankton over reefs.

Turbulence

Turbulence is greater near the bottom on reefs (Reidenbach et al. 2006). Although larval responses to turbulence are poorly known, crab megalopae can ascend in a laboratory tank when turbulence increases and descend when it decreases (Welch et al. 1999). However, many zooplankters are actually attracted to turbulence (Rothschild and Osborn 1988; Kiorboe and Saiz 1995), and their behaviors are varied and complex (Visser et al. 2009). It is unlikely that avoidance of turbulence generated the wide spread pattern observed across such disparate taxa in Moorea. Holzman et al. (2005) found no relationship between turbulence and near-bottom zooplankton depletion in the Red Sea. Moreover, visual observations of fluorescein dye released in the upper 1 m at our study site revealed no discernable difference in flow or turbulence even though large differences in plankton abundance occurred there (Alldredge, personal observation).

Food availability

Zooplankton may seek areas of higher food (DeMott and Watson 1991; Metaxas 2001). However, phytoplankton large enough to be consumed by zooplankton were more abundant nearer the bottom, opposite the trend observed for zooplankton. Therefore, it does not seem that zooplankton are being attracted to high phytoplankton abundances in the water column. Although reef environments are typically depleted in phytoplankton near the bottom (Yahel et al. 1998; Genin et al. 2002), the benthic affinity of the diatom taxa at our study sites suggests some bottom resuspension of this taxon. While microzooplankton, another important food for zooplankton, were not quantified, the relatively homogeneous distribution of small flagellates, a major food source for microzooplankton, supports the notion that zooplankton were not responding to heterogeneous microzooplankton distributions. Predatory zooplankton, such the large predatory copepod *Labidocera,* may concentrate near the surface in response to the higher prey densities found there. However, even predatory zooplankton may respond primarily to other cues. *Labidocera*, for example, accumulated on the sunward side of a bucket when captured (Alldredge, personal observation) indicating an attraction to light.

Attraction to light

Our data support light as the major cue generating abundance gradients in several of the most common taxa. Copepods were highly and significantly stratified during the day or when the moon was up, but not significantly stratified when the moon was down. Crab zoea and polychaetes also showed greater abundance near the surface when the moon was up or during the day. The elimination of a vertical gradient in zooplankton abundance during the lunar eclipse, while a strong gradient existed immediately before and after the eclipse and throughout the control night, also supports light as a cue for upward swimming.

All taxa except gnathiid isopods displayed this pattern during the eclipse. Moreover, many nocturnal taxa were more abundant during moonlit periods than in the dark again supporting strong responsiveness to light.

Innate taxis behavior

Some taxa may swim upward due to negative geotaxis or other innate responses typical of vertically migrating holoplankton. Decapod larvae, gastropod veliger larvae, and ostracods were significantly aggregated nearer the surface regardless of the presence of moonlight and were also more abundant during moonless periods. However, these taxa still redistributed throughout the water column during the eclipse suggesting that even they may exhibit some light-mediated swimming behavior.

Ultimate causes of observed zooplankton gradients

Higher predation intensity by sessile invertebrates and planktivorous fish near the bottom is probably the ultimate selective pressure leading to depletion of zooplankton near the bottom on coral reefs (Yahel et al. 2005; Holzman et al. 2005). Predation by planktivorous fish is especially intense during the daytime when plankton are more visible (Hobson 1991; Hamner et al. 1988). Most diurnal planktivorous fish forage close to shelters from their own piscivorous predators and, thus, can be an order of magnitude more abundant near the bottom (Motro et al. 2005). Motro et al. (2005) provided empirical evidence that zooplankton more than 2 m above the reef are much less likely to be consumed by fish.

Zooplankton taxa that evolved to swim upward away from the reef during the day and on moonlit nights when they are more visible to planktivorous fish would be more likely to survive and reproduce than those nearer the reef, leading to selection for upward swimming behavior. Why then were zooplankton on the deep (5–15 m) fringing reefs of the Red Sea only depleted near the bottom boundary layer (Yahel et al. 2005) while in Moorea zooplankton stratification occurred throughout the water column even on the deeper fore reef? A comparison of these systems suggests that retention on the reef might be an additional selective pressure promoting the evolution of upward swimming behavior.

Hench et al. (2008) found that the north shore of Moorea exhibits recirculation and some retention of water. This system is wave-forced with relatively little impact from tides. Water exits the lagoon through a series of deep passes and is transported back along the fore reef and over the reef crest by wave action. This sets up kilometer-scale surface circulation cells that recirculate seawater at rates dependent on the wave forcing and the strength of the alongshore currents on the fore reef. Water residence times can be as short as only a few hours at high flow rates as depicted in Fig. 13 (based on Hench et al. 2008). Thus, current patterns in this system could retain zooplankton on the reef by recirculating some of them over and over again across the back reef, out the passes, along the fore reef and back across the very shallow reef crest into the lagoon. Although this is the general circulation pattern, depending on the strength of the jet in the pass and the alongshore currents, some zooplankton would also be exported offshore.

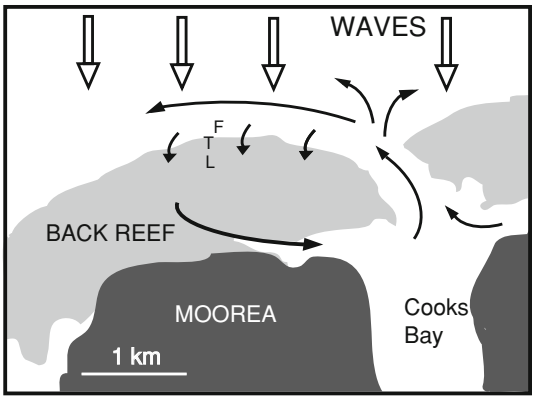

Fig. 13 Diagram of the general surface circulation during the austral summer at the study site on the north shore of Moorea, French Polynesia based on Hench et al. (2008). T = Transect; L = Lagoon; and F = fore reef sampling sites

Certainly true oceanic holoplankton is being transported onto the reef from offshore in this system. But the strong upward swimming of many zooplankton taxa toward light, opposite of the normal behavior expected of diurnally migrating oceanic zooplankton, is consistent with the physical recirculation and retention model of Hench et al. (2008). Residency on the reef over multiple generations would provide the opportunity for selection of such upward swimming behavior. If this hypothesis is correct, repeated high exposure to predation during circulation cycles may explain the low overall abundances of zooplankton at our site relative to fringing reef systems (see Table 1, Heidelberg et al. 2004) and suggests that the selective pressures to evolve behaviors that avoid the reef may be more constant and inescapable in this system than in the deeper fringing reef systems studied previously. Finally, while the surface acts as a barrier as well as a refuge in shallow water, on the fore reef, it serves as the optimum location from which to be swept by wave-driven flow back over the 20 cm deep reef crest into the lagoon due to Stokes drift. Zooplankton swimming near the surface would probably experience increased retention within the reef system. Extensive water retention and entrainment may be much less pronounced on most deep fringing reefs and there is likely less benefit for

zooplankton to swim to the surface. In these systems, high predation pressure in the bottom boundary layer 1–2 m above the reef may select only for avoidance of this particular layer (Motro et al. 2005).

It is clear that predation is a strong selective pressure with different effects in different systems. Other systems show vertical distribution patterns of zooplankton opposite of those in Moorea. Most vertically migrating open water holoplankton avoid visual predators by swimming upward to feed at night and down in the day (Hamner 1995). Hyperbenthic and demersal zooplankters over sandy bottoms and holoplankton over some non-reef habitats are in higher abundance near the bottom where they find protection from transient predators foraging higher in the water column (Alldredge and King 1985; Barans et al. 1997; Kringel et al. 2003; Carleton and Hamner 2007). These habitats are considerably different from coral reef habitats where fish predators are both abundant and associated with particular bottom features. In these reef systems, zooplankton clearly benefit by avoiding the bottom. Parasitic gnathiid isopods were the only taxon we observed that remained consistently near the bottom in closer proximity to potential fish hosts.

Zooplankton abundance and variability

Zooplankton abundances over coral reefs vary geographically from highs of 3000–4000 animals m^{-3} in Jamaica and Panama, to <100 m^{-3} on the Great Barrier Reef (see Heidelberg et al. 2004). Abundances in Moorea, ranging from <50 to about 400 animals m^{-3}, were similar to other Pacific reefs (Sale et al. 1978; Roman et al. 1990) and to other studies in French Polynesia (Renon 1978; Renon et al. 1985; Carleton and Doherty 1998). Taxonomic composition, dominated by copepods during the day and larger crustacean meroplankton at night, was also very similar to previous studies. Likewise, zooplankton biomass of 0.2 to >1.1 mg C m^{-3} was similar to the 0.5–0.9 mg C m^{-3} reported for Great Barrier Reef flats (Roman et al. 1990).

Zooplankton assemblages over coral reefs are highly variable in time and space. They are impacted by physical and biological factors such as tides, internal waves, season, rainfall, reproductive cycles, phytoplankton concentrations, swarming behavior, and predation (see Heidelberg et al. 2004 for review). As is typical for coral reefs, zooplankton on the back reef in Moorea were more abundant and taxonomically diverse at night then during the day (Emery 1968; Roman et al. 1990; Heidelberg et al. 2004; Yahel et al. 2005; Carleton and Hamner 2007; Nakajima et al. 2008). But strikingly, variability in zooplankton abundance was greater over just a few centimeters of depth than even between seasons (August vs. January) or between day and night. Moreover, lunar variability was also high, with significantly more total plankton present when the moon was up than down on the same night and highest at full moon. This consistent response to the full moon may be part of the general adaptive response to light observed among zooplankton in Moorea. Sparse lunar data from previous studies also show high abundances near full moon although these were not significantly different from other lunar phases (Heidelberg et al. 2004; Palardy et al. 2006). Corals in Moorea and elsewhere spawn within a few days of the full moon (Harrison and Wallace 1990; Carroll et al. 2006); although any relationship to higher zooplankton abundances near this time is unknown. Clearly, care must be taken in comparing abundances among lunar studies to be certain they reflect plankton from similar depth horizons.

Zooplankton <200 μm in size were not sampled in this study. Corals feed primarily on larger zooplankton >200 μm in width (Palardy et al. 2006) and planktivorous fish favor larger, more visible prey (Hobson 1991). Thus, our conclusions apply to the size fraction of zooplankton most significant as a food source for most reef planktivores.

Ecological implications

These results have significant implications for food availability to planktivores on shallow reefs. Zooplankton are especially important for the health, growth, and survival of corals (reviewed in Houlbreque and Ferrier-Pages 2009). Planktivorous corals and other sessile invertebrates could obtain substantially more food if they can feed even a fraction of a meter higher in the water column and those which can grow higher or attach to substrate higher in the water column could have an advantage over those nearer the bottom, especially in systems such as Moorea where zooplankton are scarce. Interestingly, amphipods, isopods, and zoea, which we found either did not stratify at all or were more evenly distributed throughout the water column when the moon was down, made up 79% of the zooplankton consumed by *Pocillopora* and *Pavona* spp. (Palardy et al. 2006) suggesting that the behavior of these zooplankton taxa may make them more susceptible to predation.

Preliminary results in Moorea show that transplanted corals grow faster higher in the water column and that growth is significantly correlated with the availability of crustacean zooplankton. Coral bleaching also decreased with increasing coral height above the bottom and was correlated with current speed and sedimentation rate near our study site (Lenihan et al. 2008). But greater availability of zooplankton prey may also mitigate bleaching (Grottoli et al. 2006; Palardy et al. 2008) suggesting that taller corals may have bleached less because they captured more zooplankton higher in the water column.

Planktivorous fish are a major component of coral reef communities both day and night (Hobson 1991; Holzman et al. 2007). Most diurnal planktivores, including pomacentrids and planktivorous triggerfish (Balistidae) feed primarily on copepods (reviewed by Hobson 1991) which we found to be highly concentrated near the surface. Zooplanktivorous fish have been shown to grow faster 1 m above the bottom than closer to the bottom (Clarke 1992), presumably because zooplankton were more abundant. Although planktivorous fish foraging higher in the water column are likely to obtain more food, foraging height is a trade off between risks and benefit. Thirty times more planktivorous fish occurred in a layer where prey density was half that of the layer above on a fringing reef in the Red Sea, probably because of the increased risk of predation by piscivorous fish further aloft (Motro et al. 2005).

Nocturnal planktivores including soldier fishes and cardinal fishes have large eyes to help them locate prey at night. Their major prey tend to be larger (>2 mm), often demersal forms including mysids, crab megalopae, polychaetes, decapod larvae, and large copepods such as *Labidocera* and *Pleuromamma*, primarily because they cannot see smaller zooplankton (Hobson 1991; Holzman and Genin 2005). The visual acuity of some nocturnal planktivores may increase in the presence of moonlight (Munz and McFarland 1973), but perhaps more significantly, many diurnal planktivores reappear above coral heads during bright moonlit periods (Hobson 1965), which may explain why even smaller zooplankton display vertical gradients similar to daytime distributions when the moon is up but are more evenly distributed throughout the water column when the moon is down.

Implication for sampling zooplankton near reefs

The existence of high variability in zooplankton abundance over only fractions of a meter difference in depth indicates that considerable care is needed to accurately measure zooplankton abundances and food availability to coral reef planktivores. Plankton abundance measured with nets will be highly sensitive to collection depth and zooplankton availability to reef planktivores will need to be determined as close as possible to their actual foraging depth. Moreover, repeated vertical hauls extending all the way from the bottom to the surface that do not favor any one depth will be required for comparison of average zooplankton abundances among different reefs and especially over shallow back reefs.

Clearly, the vertical distribution of zooplankton over coral reefs is highly variable and dependent upon reef characteristics such as water depth and circulation patterns as well as upon environmental variables such as light and predation pressure. Zooplankton are central players in coral reef food webs. Knowledge of their behavior and distribution are essential for a complete understanding of community dynamics in these important systems.

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